

NOTES ON THE POPULATION ECOLOGY OF CICADAS (HOMOPTERA: CICADIDAE) IN THE CUESTA ANGEL FOREST RAVINE OF NORTHEASTERN COSTA RICA*

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INTRODUCTION

Several previous field studies of cicadas (Homoptera: Cicadidae) in Costa Rica have revealed that different sympatric genera and species often exhibit allochronic (seasonal) annual adult emergence patterns and habitat associations (Young 1972; 1974; 1975a; 1976; 1980a,b,c; 1981a,b,c). Most of these studies concerned cicadas associated with lowland tropical forest and the Central Valley regions of Costa Rica, although one study in particular (Young 1975) examined some aspects of the population ecology of cicadas in a mountain forest. Because different species, and sometimes genera, of cicadas are found in different climatic and geographical regions of Costa Rica (Young 1976), it is necessary to examine the population ecology of these insects in as many of these ecological zones as possible. This paper summarizes an ecological survey of the cicadas thriving in the steep and very rugged forest ravine known as "Cuesta Angel" in the Central Cordillera of northeastern Costa Rica. The information reported here complements the studies of cicadas in other ecological zones of Costa Rica, although by no means does as extensively owing to the difficulties working on the very steep slopes of the ravine. It is shown tentatively that (a) the cicada fauna of this region includes at least two species not discussed or found in the other regions studied, (b) the resident species exhibit different annual emergence patterns, and (c) nymphal skins of several species are distributed at very low densities and in association with various genera and species of leguminous canopy-size trees in the ravine habitat.

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Fig. 1. The ravine forest at Cuesta Angel, near Cariblanco, Heredia Province, Costa Rica.

METHODS

The Cuesta Angel ravine is an extensive strip of very steep primary and river-bottom forest (Fig. 1) filtering down from the highest mountains of Costa Rica's Cordillera Central and tapering into the northeastern lowlands known as Sarapiquí. Because of its rugged profile much of the ravine remains blanketed in forest even though surrounding level areas have been largely converted to pastures. This ravine is within the recently extended Carillo National Park. There have been relatively few field studies of plants and animals in the ravine, even though both its invertebrate and vertebrate faunas contain many forms not found in other parts of Costa Rica. "Cuesta Angel" is located about 10 km south of the village of Cariblanco ($10^{\circ} 16'N$, $84^{\circ} 10'W$), Heredia Province, and is classified as montane tropical wet forest (elev. about 1200 m) (Holdridge 1967). The vertical drop in the ravine is about 300 m.

As shown by 1972 and 1973 rainfall data, the region is very wet and with a short and erratic dry season during January and February (Fig. 2). For either collections of nymphal skins or determination of species active by calling songs or collection of specimens, the locality was visited the following dates: 27–30 June 1972, 14 August 1972, 15–17 February 1973, 20–24 March 1973, 18–20 April 1973 (beginning of nymphal skin regular censuses), 22–25 May 1973, 6–10 June 1973, 4–7 July 1973, 7–9 May 1975, 3 April 1976, 1 and 5 November 1980. Dates of visit included both wet and dry periods for this region. During the April 1976 visit, Dr. Thomas E. Moore recorded calling songs of the species active at that time.

The 1973 visits were concerned primarily with attempting to census the nymphal skins of various species active at different times of the year while other dates were devoted to listening and collecting adult specimens. The nymphal skins of recently emerged cicadas are relatively easy to distinguish from those of a previous years' emergence owing to discoloration and disintegration of some parts (Young 1980a) and therefore provide an accurate record of a recent or current emergence within the year. The locations of nymphal skins in the habitat also provide information on the possible feeding associations of the nymphs in the ground and other aspects of microhabitat. I censused nymphal skins, with the assistance of at least one, and usually two, trained student assistants by marking off rectangular or square plots (usually 5×5 meters) immediately beneath a tree or other spot where at least one nymphal skin was found. Initially we crawled through the forest along transects to determine where nymphal skins were found and then marked off the trees and places having them. The transect approach was used in the survey of the very rocky terrain comprising the river-edge forest on relatively flat ground, but working on the steep slopes entailed spot-checking various places owing to the difficulty of the terrain and often very misty conditions. Thus the nymphal skin census program involved repeated censuses at twelve marked canopy-size trees on the slopes, and four large river-edge plots of forest, each plot containing many trees. The four river-edge plots, each one widely separated from the other by at least 100 meters of forest, ranged in size from 462m² to 300m², the differences being due to rivulet channels and other interruptions in the forest. With the exceptions of marked trees 2, 6, and 7 (each of which was a plot of about 90m²),

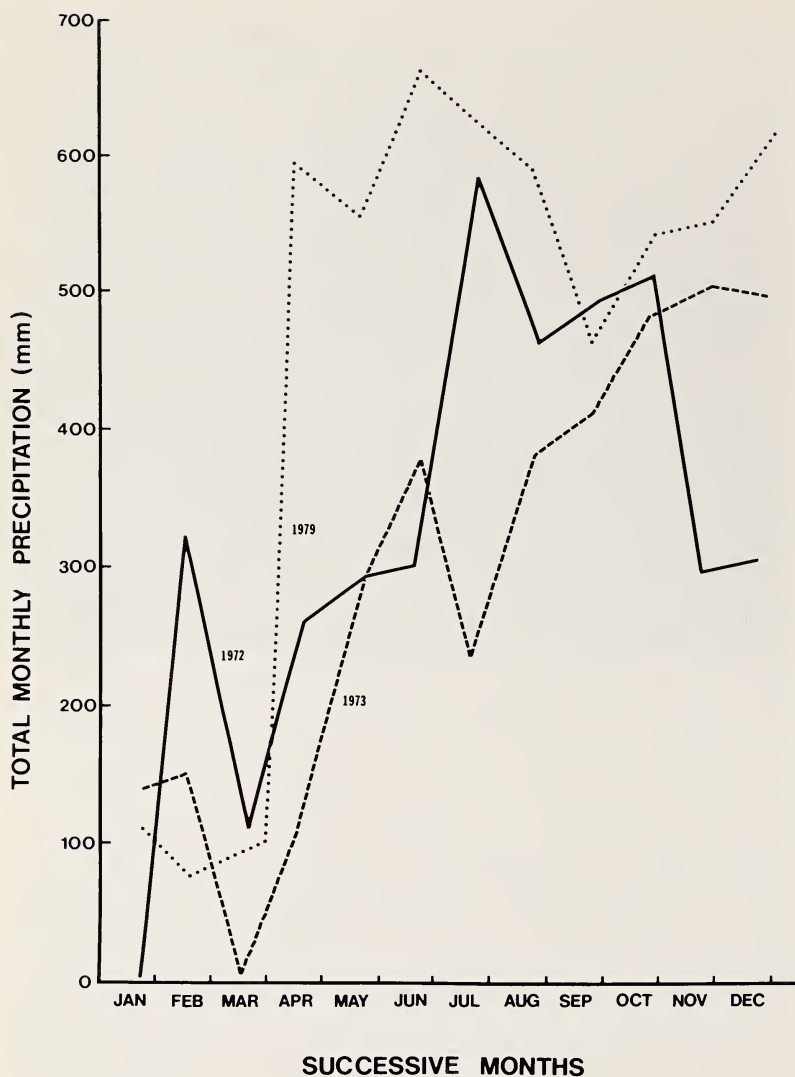


Fig. 2. A sample of three separate years of monthly rainfall patterns at Cariblanco. In all three years portrayed, a short dry spell occurs between January and March, although conditions are not completely dry as in other regions of Costa Rica with distinct dry seasons.



Fig. 3. The forest habitat at the top of the ravine, and above the Sarapiqui roadcut. The cicada *Fidicina* n.sp. is abundant here.

most tree plots on the slopes were 25m^2 . The twelve tree plots gave a total habitat area of about 484m^2 sampled for nymphal skins several times and a total of $6,957\text{m}^2$ of river-edge forest sampled as well (total sample area of $7,441\text{m}^2$). The tree plots were widely scattered with the closest being no less than 30 meters apart. The sample included the hill-top forest above the Sarapiqui roadcut (Fig. 3) as well as the forest habitat to either side of the secondary road down into the ravine (Fig. 4). A census consisted of making an exhaustive collection of all cicada nymphal skins found within each plot, including those attached to plants and tree trunks and those lying in the ground litter. The contents were placed into a plastic bag and labeled appropriately. Later the skins were determined to species and sex. The nymphal skins of the cicadas studied were readily separated to species in my field samples on the basis of marked differences in size, color, and body profile. Skins were matched with

others obtained from collecting skins when adults were emerging. In previous studies (Young 1972; 1975a; 1980a,b; 1981a,c) I have illustrated and discussed distinguishing features of cicada nymphal skins. Based upon these materials, a key to the Costa Rican cicada fauna, using both adults and nymphal skins, is being formulated (T.E. Moore and A.M. Young, in preparation). In the present study, it was very easy to distinguish nymphal skins of *Fidicina* species (three species) on clear-cut differences in color pattern and size; the *Zammara* species studied has nymphal skins very different in color and body profile from the others (see also Young 1972), while the two species of *Carineta* species had nymphal skins differing in color, even though of very similar size. One species has a very dark brown nymphal skin, and the other, light brown. Based upon matching of skins with adults done by myself and T.E. Moore, I am reasonably certain that matches of field collections of skins with adults is very reliable. Voucher specimens of fruits and leaves of the trees having nymphal skins beneath them were collected and sent to specialists for determination.

Other observations included determining the places on the ravine where adult cicadas were heard chorusing as a means of estimating preferences among species for the river-edge area and top of the ravine. In some instances, diurnal patterns of calling were also noted and the trees used for calling. Once the species were determined, records of captures of cicadas in other regions of Costa Rica were checked by examining the University of Michigan collections and data bank on Neotropical species in other museums, as a means of determining if the Cuesta Angel species were found elsewhere in Costa Rica. Because virtually nothing is known about the geographical distributions and habits of Neotropical cicadas in general, vouchers of both adults and nymphal skins were saved and placed in collections at the University of Michigan and the Milwaukee Public Museum.

Owing to the steep terrain and heavy rains of the region, a small experiment was conducted on estimating the rate of disintegration of cicada nymphal skins on both forested slope and river-edge forest. Such a test would tell me how many skins were being missed between census intervals because they were possibly disintegrated, particularly on the slopes, before the next census was taken. Thus in the May 1973 census, two groups of fresh skins of one of the larger species, each group containing ten skins, were established, one



Fig. 4. The forest habitat along the secondary road going to the bottom of the ravine. Cicadas such as *Fidicina sericans*, *F. mannifera*, and two species of *Carineta* are heard in the trees along this road.

group of a patch of forest slope where this species emerges, the other on a level area adjacent to the Sarapiquí River. The skins in each group were randomly distributed (by throwing) within a one-meter square area of ground. The numbers of skins remaining in each plot were then checked in June and July 1973.

RESULTS

The six species of cicadas found and studied at Cuesta Angel are shown in Fig. 5, and they are: *Zammara tympanum* Distant, *Fidicina sericans* Stal, *Fidicina* "new species" (n.sp.), a new species, *Fidicina mannifera* Fabricius, *Carineta postica* Walker, and *Carineta* sp. Three of these, *Z. tympanum*, *F. sericans*, and *F. mannifera*, are large-bodied cicadas with very loud calls, while *F. n.sp.* is medium-sized, and the two species of *Carineta* are considered small-sized (or at the low end of the medium-size range), the latter two

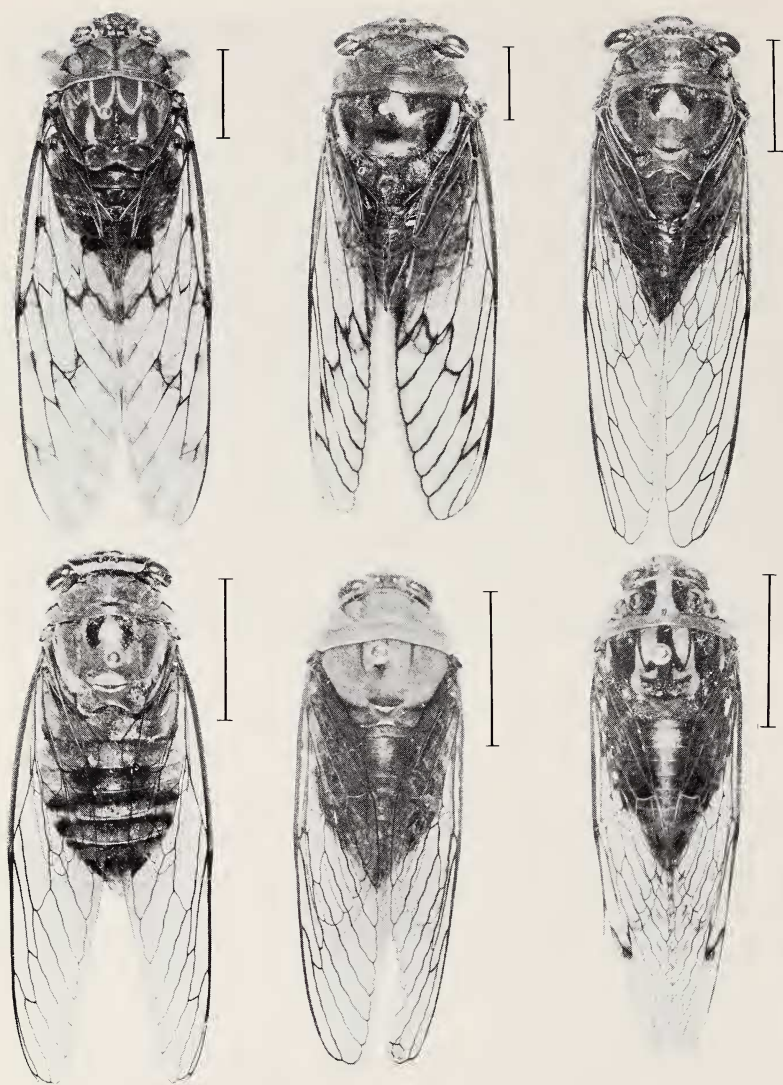


Fig. 5. Cicadas found in the Cuesta Angel ravine forest, top, from left to right: *Zammara typanum*, *Fidicina mannifera*, *F. sericans*; bottom, left to right: *F. n.sp.*, *Carineta* sp., and *C. postica*. The vertical black line to the left of each cicada gives the scale of one cm. relative to the body shown in each photograph.

cicadas having very soft calls. *Zammara tympanum* adults are heard throughout most of the year and sometimes during the dry season and they call from the moss and other epiphyte-covered trunks of forest trees primarily along the river-edge. This cicada is mottled green and brown and has brown spots on the wings, immediately distinguishing it from the others. The call is a "winding up-like pulsating buzz. Adults when calling occur at one per tree, and there are usually no more than two or three calling males present within approximately 800m² parcels of river-edge forest during an optimal calling period. Males call throughout the day, including overcast and light drizzle conditions. Males are bright green with brown markings while females are drab olive green and brown.

Fidicina sericans, both sexes, are black with green markings on the thorax and smoky wings. The call is a steady rather high-pitched buzz most frequently heard during sunny weather and during the dry season. Sometimes several males congregate in the same tree, particularly if it is along an edge of forest, and sometimes, under these conditions, several adjacent exposed trees may have males calling at the same time. The calling males are seen perched on the upper portions of the trunk and on branches, and they are easily spotted on light-colored bark species such as *Pourouma* and *Cecropia*. Adult densities, as indicated by calling males, probably are about 1–20 cicadas per 800m² of forest during a period of peak calling, although this may be an underestimate since only a fraction of males may chorus at any one time. Calling males are heard primarily on the forest slope and less so at the bottom of the ravine and at the very top.

Fidicina n.sp., both sexes, possesses a green head and thorax and black and orange-banded abdomen, sometimes with patches of silvery hairs laterally. Of all of the cicadas in Costa Rica, this species is the most difficult one to catch because of their habit to perch very high in trees and to change trees after one call. Based on comparisons with type materials and other specimens, this is most likely a new species. It has a very distinctive two-part call: the first part is a series of pulsating chirps followed by a longer period of siren-like and pulsating calls. Unlike this species, both *Z. tympanum* and *F. sericans*, as well as the other species to be discussed, often make repeated complete calls from the same perch, even if interspersed with periods of silence lasting several minutes or an hour or two. *F.* n.sp. is heard during the dry season and it occurs in the ravine and

above the Sarapiquí roadcut. Adult densities appear to be very low, similar to that of *Z. tympanum*, but difficult to determine due to the highly mobile habits of males.

Fidicina mannifera, both sexes, is dark brown with some dark green markings on the head and thorax and with tinges of brown along the veins of the wings. The body is very pubescent. Males generally call at dusk and dawn and usually for about 15–20 minutes during each period. The call is a very intense pulsating shrill buzz. Based upon observing a total of close to 20 individuals at this locality, there is about a 50:50 chance that a male just completing a call will stay in the same tree. Males are heard primarily inside the forest and on the lower slope and along the river. Densities are very low with probably only one or two males per 1000m² of forest habitat.

Carineta postica, also illustrated in Young (1975), is black with green markings on the head and thorax and with the entire body blanketed in setae. The wings are smoky and calling males have the habit of perching head-downward on the trunks of forest trees, a behavioral trait separating the larger-sized members of the genus from all other Neotropical cicadas. Males sing from moss-covered tree trunks and branches inside the river-edge forest and along the river itself. Densities are low, with 1–5 calling males per 500m² of forest and with calling limited to the late afternoon or overcast conditions during the dry season. The call consists of repeated coarse “zip-zip” sounds, and is reminiscent of a muted version of the call of the familiar cone-headed grasshopper of North America. This species may also be *C. trivitatta* Walker as specimens of both species are very similar in size and coloration. Clarification awaits further study.

Carineta sp. is pea-green with clear wings and calls from forest edge trees such as *Cecropia* during the wet season. It is of same size and profile as *C. postica* but is most abundant near the top of the ravine. The call is also similar to that of *C. postica* but somewhat louder and calling is generally a dusk phenomenon. Sometimes as many as eight males have been seen perched at different heights on the trunk of the same *Cecropia* tree.

The data on temporal emergence patterns annually from the censuses of nymphal skins present a more diffuse picture of seasonality in the cicadas at Cuesta Angel (Fig. 6). Caution is given here in that these data are very fragmentary and discontinuous,

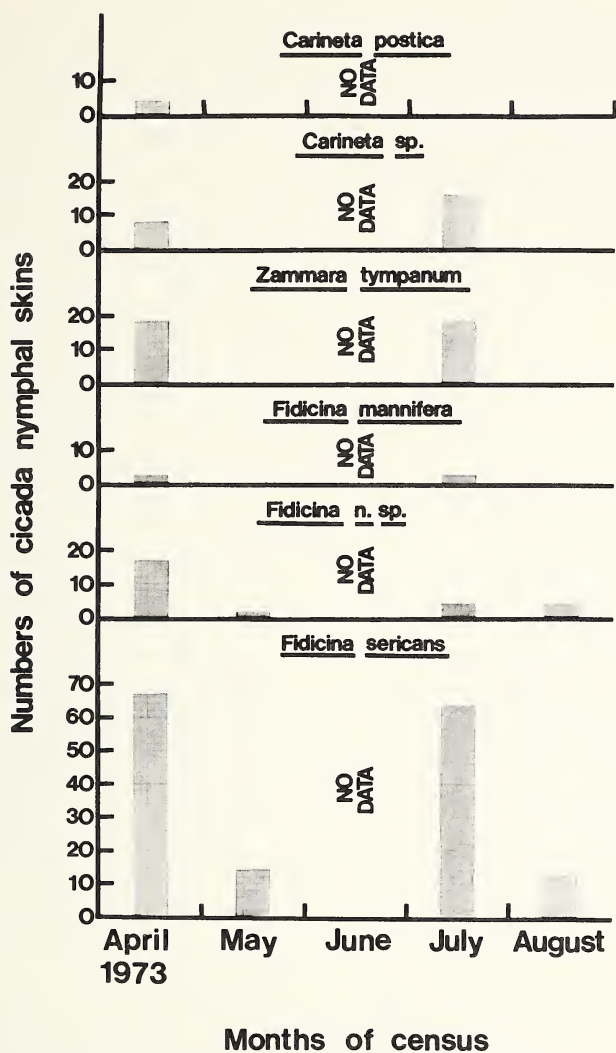


Fig. 6. Monthly collections of cicada nymphal skins from tree plots and river-edge plots at Cuesta Angel.

although the best there are at this time. With the exception of *C. postica*, there appears to be a trend for most species to emerge during both wet and dry seasons, when considering both the nymphal skin and call records together. Thus although *F. sericans* is heard in abundance during the short dry season, there is some evidence of emergence well into the wet season (Fig. 6). But examining the 1973 rainfall data shows a marked dip in rainfall during July (Fig. 2), giving a brief dry spell that month. If it is assumed that the data are actually representative of emergence patterns of cicadas at Cuesta Angel, it then appears that another dry season species, *C. postica*, did not respond to the July 1973 dry spell as there was no emergence (Fig. 6). At the same time, the dry spell was apparently insufficient in intensity to block the emergence of wet season species such as *Z. tympanum*. Perhaps even more interesting is the wet season emergence of another supposedly dry season species, *F. n.sp.* (Fig. 6). Adults of such species were not heard at these times although my sample sizes are very small. Different patterns of emergence may be associated with different years in which monthly rainfall regimes are very different. For example, during 7–9 May 1975, there was an abundance of *F. n.sp.* calling in the ravine as was the case for 4–7 July 1973. Both of these months, in different years, were drier than in other years, and the rainfall data for 1972 and 1973 clearly show the year-to-year variation in monthly rainfall patterns at this locality (Fig. 2). Furthermore, when *F. n.sp.* emerged during the wet season, calling was restricted to the dry periods of the day. All of the cicadas studied exhibit bursts of calling near dusk (see also Young 1981b).

The distribution of nymphal skins for each species studied by marked trees is given in Table 1. Even though approximately 70 species of canopy-size trees were included along the initial transects to determine the locations of cicada emergence patches in the ravine, patches were found to be confined to the species of Leguminosae listed in Table 1. Note that the estimation of relative abundance of adults among the species discussed above is confirmed here in terms of nymphal skins: by far the most abundant species is *F. sericans*, whose nymphal skins comprised almost 64% of the total 241 skins collected in the 1973 survey of tree plots alone (Table 1). *F.n.sp.*, *Z. tympanum*, and *Carineta sp.* are about evenly distributed in terms of abundance of nymphal skins in the tree plots. As in previous studies of cicadas in Costa Rica, sex ratios are close to

Table 1. Census history of cicada nymphal skins in legume tree plots* in the forest ravine, "Cuesta Angel", near Cariblanco, Heredia Province, Costa Rica.

Tree No. and Species**	Distributions and Abundances of Nymphal Skins per tree over all census dates					
	<i>Fidicina sericans</i>	<i>Fidicina n.sp.</i>	<i>Fidicina mannifera</i>	<i>Zammara tympanum</i>	<i>Carineta sp.</i>	<i>Carineta postica</i>
(1) <i>Pithecocolobium latifolium</i>	0	0	0	0	4	0
(2) <i>P. latifolium</i>	72	7	1	13	1	0
(3) <i>Inga sp.</i>	13	1	0	3	0	0
(4) <i>Pithecocolobium sp.</i>	1	0	0	0	0	0
(5) <i>Inga sp.</i>	1	3	1	0	1	1
(6) <i>Inga sp.</i>	34	2	0	0	0	0
(7) <i>Pentaclethra</i>	6	4	0	1	4	0
(8) <i>Inga sp.</i>	7	0	0	7	0	2
(9) <i>Platifolium</i>	0	0	0	1	2	0
(10) <i>Inga sp.</i>	4	5	2	4	10	0
(11) <i>Inga edulis</i>	15	0	0	1	0	0
(12) <i>Inga enfusa</i>	0	1	0	5	1	0
(12) <i>Inga edulis</i>						
Total skins	153	23	4	35	24	3
Range per tree	0-72	0-7	0-2	0-13	0-10	0-2
Mean ($\bar{X} \pm S.D.$)	12.75 ± 21.07	1.91 ± 2.35	0.33 ± 0.65	2.91 ± 3.91	1.91 ± 2.93	0.25 ± 0.62

* Each plot ranged in size from 5×5 meters to 10×9 meters around the base of individual legume trees.

** All trees and cicadas were censused 18-20 April, 22-25 May, 4-7 July, 15 August 1973 (total of 14 days), except for trees 9, 10, 11, and 12, which were added to the census program on 4 July 1973.

unity. Taking the most abundant species, *F. sericans*, there is considerable range in numbers of skins found in the different tree plots, although close to 40% of all skins of this species were found beneath one individual of *Pithecollobium latifolium* (Table 1). Yet a second individual of this tree species yielded only four skins of cicadas overall and none of *F. sericans*. Such data, although limited, indicate the considerable variation encountered over different patches of the same resource for a cicada species in tropical forests. Two different individuals of *Inga* and one *P. latifolium* together account for almost 65% of all skins found. That such data may be underestimates of true values, even for an abundant species such as *F. sericans*, is suggested by the results of the estimate of rate of disintegration of nymphal skins: at the end of a five-week period, between 50% (level ground) and 80% (slope) of the *F. sericans* nymphal skins studied had disappeared. These samples are pitifully small, but it is the best we have at this time. The intervals between censuses in my study are of this magnitude and greater, thereby indicating the likelihood that some skins were missed owing to their rapid disintegration under very wet conditions. The examination of nymphal skin distributions by tree plots and river-edge plots separately provides further confirmation of the data shown in Table 1 (Table 2). Although high percentages, if not all, of plots are occupied by skins of *Z. tympanum*, the emergence is one of very low density since only a small number of skins occur in the plots studied (Table 2). The tree plots, although only representing an area of about 6.5% of the combined area of tree plots and river-edge plots, account for almost 80% of all skins recovered (Table 2). The larger river-edge plots include a wide variety of tree species whereas the tree plots each include one individual of a leguminous tree species and understory plants. Most striking is the relatively high density of the nymphal skins of *F. sericans* in the tree plots, almost 0.4 skins/m² (Table 2). Yet the same cicada, in a much larger and representative tract of forest, representing an area about five times that of the tree plots, has the very low density of about 0.010 skins/m² (Table 2). Other patterns of nymphal skin density between tree plots and river-edge plots are self-evident and support the pattern discussed for *F. sericans* (Table 2). From such results, one can readily appreciate the distortion of density estimates when different size patches of the environment, with different biological attributes, are combined to give a summary figure (Table 2). And

Table 2. Some population parameters of cicada species in the ravine forest, "Cuesta Angel", Costa Rica

Cicada Species	Body Size (mm)	Distribution and Abundance of Nymphal Skins					
		River-Edge Plots (4)*			Tree Plots (12)***		
		Total Skins	# Plots with Skins	Density**	Total Skins	Ratio Occupied Plots	Density
<i>Zammaratympanum</i>	28 mm	10	4	0.001 m ²	35	8	0.106 m ²
<i>Fidicina sericans</i>	31 mm	21	1	0.010 m ²	154	9	0.377 m ²
<i>Fidicina</i> n.sp.	25 mm	7	2	0.002 m ²	23	7	0.064 m ²
<i>Fidicina mannifera</i>	39 mm	1	1	0.004 m ²	4	3	0.024 m ²
<i>Carineta postica</i>	10 mm	3	3	0.001 m ²	3	2	0.060 m ²
<i>Carineta</i> sp.	18 mm	9	3	0.002 m ²	23	8	0.060 m ²
							0.005 m ²

*There are four river-edge plots of these sizes: 2,145m², 1,350m², 462m², and 3,000m² for total area of 6,957m².

**All estimates of density based on occupied plots only; no empty plots included.

***Most of these plots are 25m² for a total area of 484m².

the data also show, that for larger areas of environment as typified here by the river-edge plots, there are not necessarily going to be increases in densities of insects recovered.

DISCUSSION

Of the six species studied at Cuesta Angel, none are exclusive to the locality, but other locality records from Costa Rica indicate similar elevations and habitat. *Fidicina* n.sp., *Zammara tympanum*, and both species of *Carineta* have been collected at Turrialba, Cartago Province as shown by specimens in the collections at The University of Michigan Museum of Zoology. The species I term *C. postica* may also be *C. trivitatta* Walker, which has also been collected from the San Jose area, Guapiles (Limon Province) and Bajo La Hondura (San Jose Province). Two other cicadas, *F. sericans* and *F. mannifera*, have much more extensive ranges in Costa Rica as both have been collected and studied in premontane and lowland tropical wet forest regions of the Atlantic coastal watershed (Young 1972; 1980b), and *mannifera* also occurs in the semi-dry to dry forest region of the western provinces of Puntarenas and Guanacaste (Young 1981a,c). Given the topography of the Cuesta Angel region relative to the adjacent lowlands, it is not surprising to find species such as *sericans* and *mannifera* along a more or less continuous elevational gradient within the wet forest region and over a range of about 90–1100 meters. Yet this is not true for the genus *Zammara* or *Carineta* since entirely different species occur in the adjacent premontane and lowland wet forest regions of northeastern Costa Rica (Young 1972; 1976; 1980b). From both records of adults calling and nymphal skins, both *sericans* and *mannifera* occur at much lower densities in the Cuesta Angel montane wet forest than they do in adjacent premontane and lowland wet forests. Given these records, it is concluded tentatively that cicadas such as *F. n.sp.*, *Z. tympanum*, and the two species of *Carineta* studied are montane species associated with wet forests while *F. sericans* and *F. mannifera* are lower elevation forms also associated with generally wet forests and semi-dry forests. Thus the Cuesta Angel cicada fauna is a mixture of montane and lower elevation tropical wet forest cicadas.

Both generic and specific richness of cicadas at Cuesta Angel are not as high as they are in the adjacent lower elevations. There are six

genera and about ten species of cicadas found in the adjacent premontane tropical wet forest (Young 1980b) as studied about 25 km from the Cuesta Angel locality. Young (1975) found only two genera, each monospecific, at another montane wet forest locality, Bajo La Hondura. There are also greater numbers of genera and species found in mid-elevation moist forest (Young 1980a) and lowland tropical dry forest (Young 1981a) in Costa Rica. Cicadas such as *F. sericans* and *F. mannifera* are tentatively interpreted as being ecological "leaks" into the forested ravine at Cuesta Angel. Given the continuous accessibility to lower elevation wet forest habitats moving along the ravine into the lowlands, it is unreasonable to expect some highly mobile insects to colonize at either end (Young 1975b).

Elsewhere in Costa Rica, cicadas have been found to have distinct seasonal patterns of adult emergences each year (Young 1972; 1975a; 1980a,b; 1981a,c) with the recognition of usually three kinds of cicadas: dry season, wet season, and transitional forms between dry and wet seasons. From the studies of cicadas in premontane tropical wet forest in particular (Young 1980b), however, it became apparent that brief spells of wetness in a dry period and of dryness in the wet season may trigger emergence of wet season and dry season species respectively. In the premontane tropical wet forest zone of northeastern Costa Rica, typically wet season cicadas such as *Z. smaragdina* Walker will emerge in low numbers during a rainy spell of about five days or longer within the dry season (Young 1980b: pers. obs.). During a dry spell within the long rainy season at the same locality, *F. sericans*, a typical dry season cicada, can also be heard and fresh nymphal skins found (Young 1980b: pers. obs.). Such observations indicate that "seasonality" in tropical cicadas is a very flexible sort of emergence strategy, perhaps determined by critical periods of wetness or dryness, depending upon the species and locality. Such an effect may explain the anolamous emergence of *F. sericans* in the wet season at Cuesta Angel. The data from Cuesta Angel very tentatively provide additional support for this phenomenon, as shown for species such as *F. n.sp.* The proximal cues triggering emergence in tropical cicadas have not been studied to my knowledge, although some ideas have been suggested for study (Young 1975; 1980a,b; 1981a). What are also needed are detailed studies of the effects of small changes in air temperature and humidity, and light intensity on the behavior of adult cicadas in

the tropics over a typical diurnal cycle. Different species may possess different levels of physiological capacity to cope with stressful environmental conditions imposed by either too much wetness or too little wetness. From my work on cicadas in Costa Rica over the past eleven years, and particularly from data on densities of nymphal skins of co-occurring species in the same patches of habitat, it seems doubtful that seasonal emergence patterns in cicadas is related to interspecific competition in developing cicadas. From what little information I have, there is little reason to suspect competition for oviposition sites. But the great diversity in the properties of the calling songs among co-occurring species in tropical forests, and the tendency for several species to form single species aggregates of chorusing males (Young 1980c) suggest that there might be competition for optimal calling conditions. In cicadas, the calling song is a major component of fitness since it presumably functions in mating, and there might be strong selection to evolve allochronic emergence patterns when the calling songs of species conflict and reduce mating success. Certain types of seasonal changes in the environment, yet to be determined, may provide the most ready cues for these insects to exploit in evolving allochronic emergence patterns to reduce losses in mating success. The whole system warrants considerable detailed study as it involves different stages in the life cycle. Seasonal emergence may or may not have anything to do with conditions being intrinsically optimal for a certain species in a certain region at a certain time of the year. If the latter, the cicada is merely locking in to a convenient cue since, under this hypothesis, both wet and dry periods provide suitable resources for adults, including those associated with mating needs.

Under the mating conflict hypothesis, it is implied that cicadas with very low densities and with unusual calling habits may forego entering into such a selection arena, thereby circumventing this adaptive pathway and emerging throughout most of the year, other things being equal. A typical case in point is the almost catholic habit of *F. mannifera* to sing for a brief period at dusk and under conditions of low population densities in Costa Rica (Young 1972; 1980b; 1981b; this paper). The intensity of the presumed mating conflict is considered to increase as population densities of co-occurring species increase individually.

In virtually all other regions studied, the greatest numbers of cicada nymphal skins occur beneath adult legume trees (Young

1972; 1980a,b; 1981a,c) although precise data on the abundances of skins in legume plots versus non-legume plots is still lacking. At Cuesta Angel cicada nymphal skin patches too were found beneath legume trees. If legume trees provide some form of highly suitable environment for developing cicadas in tropical forests, emerging populations each year will be spatially disjunct according to the spatial distribution of the legume trees whose root crowns provide a primary resource for developing nymphs. The suitability of Leguminosae for developing cicadas may involve both physical and chemical properties of the classes of root sizes exploited by various age-classes of nymphs. The observed low densities of nymphal skins in all of the plots at Cuesta Angel, relative to previously obtained densities of the same or similar species in other regions (e.g., Young 1980a,b; 1981a), may therefore be a function of the very dispersed condition of the legume trees at this locality. A striking contrast is made with the association of nymphal skins of species such as *Z. smaragdina* and *F. sericans* in relatively large patches of adult *Pentaclethra macroloba* in nearby premontane tropical wet forest (Young 1980b). Densities of these cicadas range from 5.4 to 9.3/m² in patches of two or more *P. macroloba*, estimates considerably greater than for the same species at Cuesta Angel. I interpret such observations to be the result of *P. macroloba* occurring as clumps of several trees thereby increasing the size of a single resource patch for cicadas, which results in either greater oviposition in the patch or greater survival of nymphs, or both. The river-edge plots in the Cuesta Angel study illustrate quite well such an effect. Such plots, although quite large, only contained one or two widely scattered legume trees and not clumps of such trees, and some did not contain legumes at all but were situated near such trees. The observed very low densities of cicada nymphal skins in these large segments of forest is due to an absence or scarcity of suitable root crowns for cicadas. The tree plots, on the other hand, although very small, are highly suitable for cicadas and therefore densities are high.

The pattern of cicada nymphal skins being associated with legume trees in tropical forests can have other explanations as well, ones not involving a presumed coevolved interaction of the sort suggested above. For example, selective logging of tropical forests may leave behind the relatively soft-wood legumes thereby increasing their relative abundance as a resource for insects such as cicadas. Thus the likelihood for an ovipositing cicada to discover a legume tree

increases greatly over a period of years, even though the root crowns and other cicada-related characteristics of other trees are equally suitable for cicada development.

Since all plots were located at or within the lower one-fourth of the ravine, the instances in which some species, such as *F. n.sp.* and *Carineta* sp. call primarily from the top of the ravine and not at the bottom suggests a behavioral response associated with mating requirements. Such species presumably emerge near the bottom of the ravine and fly up to the top for courtship. Such species may also emerge near the top as well although this was not determined in this study. The observed patterns of adult calling sites within the ravine are presumably related to the acoustical and thermoregulatory needs of each species.

SUMMARY

The genera and species of cicadas, their seasonal distributions, habits, and emergence sites were studied discontinuously over several years at the Cuesta Angel ravine, a rugged mountain tropical wet forest locality in the northern portion of the Central Cordillera of Costa Rica. Emphasis was placed on determining the distribution of cicadas down one steep forested side of this approximately 300-meter deep ravine and along a representative portion of its bottom (Rio Sarapiquí). Some evidence of seasonal fluctuations in abundance was obtained for the six species found here, and the greatest densities of nymphal skins of all species were found in small plots around individual legume trees. Densities in the large river-edge plots, containing many different kinds of trees, were relatively very low. The data are compared to similar data on cicadas from other regions of Costa Rica. Tropical cicada seasonality, interactions with Leguminosae, and possible mechanisms underlying population densities, are discussed.

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